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Nesting Biologies and Immature Stages of the Rophitine Bees (Halictidae) with Notes on the Cleptoparasite *Biastes* (Anthophoridae) (Hymenoptera: Apoidea)

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CONTENTS

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ABSTRACT

Information on the nesting biology of the ground-nesting *Sphecodosoma dicksoni* (Timberlake) and *Conanthalictus conanthi* (Cockerell) from the southwestern United States is added to previously published data to provide an understanding of nest architecture, cell construction, provisioning, egg deposition, larval feeding behavior, cocoon construction (in the case of *S. dicksoni*), larval defecation, and voltinism of these species. No cleptoparasitic bees are associated with either species at present.

Observations on nest provisioning and larval adaptations of the related Palearctic *Rophites trispinosus* Peréz are included. Recovery of an intermediate-stage larva of *Biastes emarginatus* (Schenck) (Nomadinae: Biastini) from the nest establishes this host association of the cleptoparasite. Its larva and the mature larva of the related genus *Neopasites* are compared and are found to share many derived features. Based on information presented here and on published and unpublished accounts, a synopsis of the biology of the Rophitinae is presented based on 7 genera and 14 species. The synopsis identifies features that seem to be characteristic of the subfamily.

The mature larvae of the Rophitinae are characterized on the basis of six genera, and a key to available species is presented. The mature larvae of *Sphecodosoma dicksoni* and *Conanthalictus conanthi* are described taxonomically and compared with larvae of other Rophitinae. Also treated is an immature larva (probably last instar) of *Rophites trispinosus*. Whereas the mature larvae of *S. dicksoni* and *R. trispinosus* share many features with rophitine genera *Dufourea* and *Xeralictus*, that of *C. conanthi* is very different, though clearly sharing significant synapomorphies with the others. Many of its differences appear to be related to the fact that it does not spin a cocoon. The pupa of *S. dicksoni* is also described, the first such treatment for any member of the subfamily.

New information on nesting biology and immatures of the rophitines, though supporting the monophyly of the subfamily, does not seem to demonstrate phylogenetic linkages with the Halictinae and Nomiinae or with the Andrenidae and Melittidae at this time. However, a number of characters are identified and discussed that may eventually be helpful in resolving these relationships.

INTRODUCTION

This paper is an attempt to increase our understanding of the nesting biology and immature stages of the Rophitinae (= Dufoureinae), one of the three generally recognized halictid subfamilies. Such information will eventually contribute to an understanding of the relationships of the rophitines to the other subfamilies of Halictidae and to other taxa.

The research started as a reinvestigation of the nesting behavior and ecology of *Sphecodosoma dicksoni* (Timberlake) and *Conanthalictus conanthi* (Cockerell). Nests of both species had been briefly studied earlier (Rozen and McGinley, 1976), but so much new information resulted from the current research that an expanded presentation of their biology seems appropriate. In addition, larvae and pollen-nectar masses of *Rophites trispinosus* Peréz preserved in the American Museum of Natural History (AMNH) allowed interpretation of some aspects of the biology of this species in light of what is known of the other two species. The new information on these species, when combined with accounts of the biology of other Rophitinae, permits a formal (but tentative) overview of the biology of the subfamily for the first time.

Larvae of only a few taxa of rophitines have been described and the account of the pupa of *Sphecodosoma dicksoni* below is the first treatment of any pupa of the subfamily. To date mature larvae of only *Dufourea* (Torchio et al., 1967 [incomplete]; McGinley, 1981, 1987; and Eickwort et al., 1986) and *Rhophitoides* (Enslin, 1921) of the approximately 12 or 13 recognized genera have been treated. In addition, Batra and Michener (1966) treated the immature larva of *Systropha*.

The manuscript for the present paper was initiated as a study of the nesting biology and immatures of *S. dicksoni*; data on the other two taxa were subsequently added and compared with information on *S. dicksoni*. This, and not presumed relationships, accounts for the sequence of presentation of the taxa here.

Acknowledgments

I thank both George C. Eickwort and Ronald J. McGinley for carefully reviewing this

manuscript and offering a number of thought-provoking suggestions.

Roy R. Snelling kindly provided a copy of a manuscript prepared by him and G. I. Stage on the nest and larva of *Xeralictus timberlakei*. He also graciously donated the single known larval specimen of this species to the AMNH, thus permitting me to examine it first hand. George C. Eickwort loaned the larva of *Dufourea novaeangliae* (Robertson) and thereby added to the completeness of the study. I extend my appreciation to Richard H. Kruzansky who analyzed the soil from the nesting area. Noel Holmgren, of the New York Botanical Garden, identified the *Nama* associated with *Conanthalictus conanthi*.

Andrey Sharkov and Beatrice Brewster assisted by translating some of the foreign literature.

NESTING BIOLOGY OF THE ROPHITINAE

Sphecodosoma dicksoni

The biology of this species was studied by Rozen and McGinley (1976) (*Sphecodosoma* then considered a subgenus of *Conanthalictus*) at 21 mi south of Animas, Hidalgo Co., New Mexico, in August 1975. Information in the earlier report agrees in most respects with the new data, but differences that do occur are discussed within the description. Measurements, counts, and other information in brackets are data from the 1976 report, presented here for comparison.

Description of Site: The nesting site of *Sphecodosoma dicksoni* was studied at 18 miles west of Blythe, Riverside County, California, on April 30 and May 1, 1992, and was again examined on May 11, 1992. This locality has been visited by entomologists from the early 1950s to the present and was referred to as Hopkins Well on some early specimen labels. The dominant feature of the site is the loose sand dunes that, though somewhat lower, have remained virtually stationary for the last 40 years. Although the dunes support little vegetation, adjacent areas are dominated by *Larrea tridentata*, other woody plants, and at the time of the current study *Sphaeralcea* and *Nama* sp. (probably *hispidum*), the latter being the food source for *Sphecodosoma dicksoni*. Precipitation in the area comes primarily in winter, resulting in a spring blooming period. During dry years the area is without bloom, but the precipitation of the 1991–1992 season was copious, and the flowering abundant. Although the sand-dwelling *Oenothera* was past bloom and *Larrea tridentata* had nearly finished flowering at the April 30–May 1 visit, *Nama* appeared to be at maximum flower. The plant was still blooming on May 11 although there were fewer flowers and a reduced number of bees visiting the plant. In addition to *Sphecodosoma*, the following bees visited the plant: *Calliopsis (Micronomadopsis) foleyi* (Timberlake), *Perdita (Pseudomacrotera) turgiceps* Timberlake, *P. (Heteroperdita) arenaria* Timberlake,[2] and *P. (Perdita) flavicauda formosa* Timberlake.

Sphecodosoma dicksoni nested in a sparsely vegetated area at the base of the east side of the sand dune. The nest entrances were interspersed with the low-growing (ca. 15 cm high) *Nama* plants. Although the patches of plants were scattered along the east side of the dunes as well as elsewhere in the region, nests were found only in two areas. The one site studied (fig. 1) consisted of a loose aggregation of nests, approximately 10 in an area of 1.5 × 0.5 m with other nests scattered farther away. The other aggregation, 30 m away in an ecologically similar area, suggested that, if time had permitted, nests might well have been found at the bases of other sand dunes where there were sufficient numbers of plants to support the foraging needs of the females.

The plants and nests were in low elevations adjacent to the sand dunes, where the ground sloped about 15° [20–30° in the 1976 study in New Mexico]. This low slope gave the impression that the species prefers horizontal nesting surfaces, but observations on the nests presented below indicate otherwise. Loose on the surface, the soil was firmer below, especially where cells were encountered, but could easily be excavated with a penknife. The surface was generally unshaded during the day. The soil, a loamy sand without peb-

[2] Specimens of this species were found on *Nama* only on May 11 by which time the flowers of *Coldenia* (its normal food source) had dried up.

Fig. 1. Nesting site of *Sphecodosoma dicksoni*, 18 mi west of Blythe, Riverside Co., California. Nest entrances most abundant to the right of the umbrella shadow.

bles and containing few roots, consisted of the following: 82% sand, 11% silt, and 7% clay. Its calcium content was high (200+ ppm) which according to Kruzansky (in litt.) probably accounted for its firmness, because aluminum (trace) and clay contents were low.

NEST ARCHITECTURE (fig. 2): All nests observed here were occupied by single females, whereas some at the New Mexico site had been occupied by two or three females. The open entrances (N = 7) penetrated into the slope of the surface at a low angle, somewhat less than 20° from horizontal. A number of females tried (some successfully) to initiate tunnels in the vertical face of the excavation I made to examine other nests. These facts as well as the low descent rate of the upper parts of main tunnels indicate that females prefer surfaces that enable them to penetrate the soil obliquely, as was also suggested at the New Mexico site.

Tumuli of loose soil accumulated on the downhill side of entrances. Generally low, some tumuli were approximately 3 cm long and 2 cm wide at maximum width. They were sufficiently more vivid in color than the surface sand, permitting easy identification of likely nests.

Main tunnels (fig. 2), 2.0 mm in diameter, turned from side to side as they slowly descended; below 10 cm, though still meandering, their paths tended to become more vertical. Open above, they were partly filled with loose sand in their lower reaches. This material could be blown away with an aspirator because the substrate below 12–14 cm was faintly moist and more consolidated.

Laterals, of approximately the same diameter as the main tunnel, extended horizontally from the main tunnel and generally ended in linear series of cells. Lengths of these filled laterals were 10–25 mm (N = 5) [7.0–13.5 mm, N = 6]. However, two laterals, both the lowest in their respective nests, ended in single cells. These cells were apparently the first of a series yet to be constructed, and their laterals were open and 45 and 46 mm long. Completed laterals were soil-filled and could

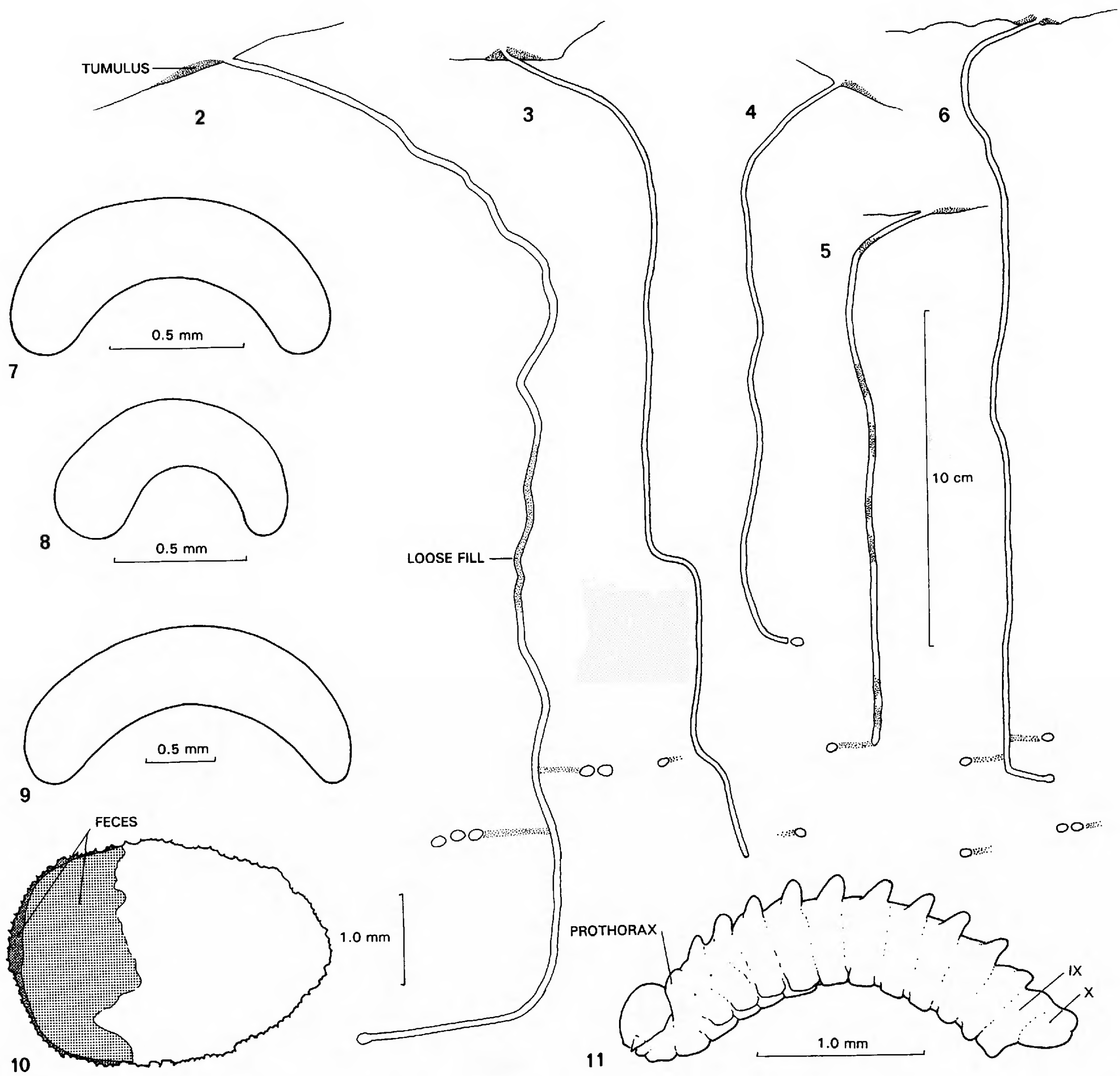


Fig. 2. Nest of *Sphecodosoma dicksoni*, side view. Figs. 3–6. Nests of *Conanthalictus conanthi*, side views. All nests drawn to same scale as indicated. Figs. 7–9. Eggs. **7.** *S. dicksoni*. **8.** *C. conanthi*. **9.** *Rophites trispinosus*. Eggs drawn to different scales as indicated. Fig. 10. Cell of *C. conanthi* side view, showing fecal deposition. Fig. 11. Young larva of *S. dicksoni*, side view.

not be detected except by the fill being somewhat softer than the substrate.

All cells in linear series (fig. 2) were more or less end to end. The only exceptions were single end cells of a new series under construction. Completed series consisted of 2 to 4 cells (N = 8) with cells of a series being uniformly spaced. Cell partitions were approximately 1 mm in the middle and 2 mm at the periphery. No intercalary spaces, either filled or empty, were noted between cells in series.

In sharp contrast to the many cell series found at the California site, cells at the New Mexico site had all been arranged singly.

Series ranged in depth from 20 to 33 cm (N = 9). Completed nests obviously consisted of a number of cell series at various depths. Although no complete nests were excavated, an incomplete one contained cell series at the depths of 24, 26, and 29 cm and another at 25, 27, and 33 cm. A nearly complete nest had a series at 16 and 21 and two series at 24 cm. Deeper cell series were always younger

than series above them, indicating that nest-cell arrangement was progressive ramifying-linear sensu Malyshev (1935). Cell depths at the New Mexico site were much shallower, 10–14 cm (N = 12).

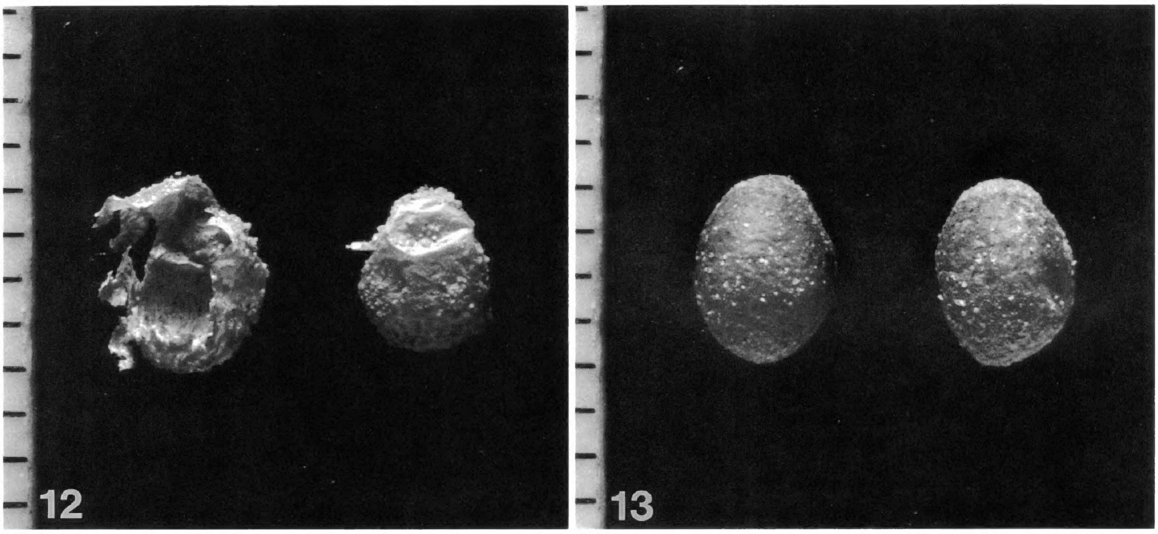
Cells were uniform in shape, rounded at the rear, with a maximum length of 4.0–4.5 mm (N = 11) [4.0–5.0 mm, N = 3] and a maximum diameter of 3.0–3.1 mm (N = 12) [3.0 mm, N = 3] somewhat to the rear of the midpoint of the long axis of the cell. Although cells in a series were essentially arranged end to end, there was some variation in this orientation. This variation in conjunction with their small size made it difficult to judge whether or not they were symmetrical around their long axis, especially because cell series were excavated from the top rather than from the side. Cells were arranged nearly horizontally with the front end slightly higher than the rear, but at the New Mexico site they tilted to the rear at about 30°.

Cells lacked walls distinctly harder or different in texture from the substrate. They were coated with an essentially invisible lining that tended to glue together the sand grains on the cell surface, making it semiwaterproof. When a droplet of water was placed on the surface, it was absorbed slowly over a period of 5 to 10 sec, in contrast to an immediate absorption of a water droplet placed on the surface of a piece of substrate. The cell surface, as at the New Mexico site, was nonreflective and not darker than the substrate. The surface was, however, more regular than the broken face of a clod of substrate. There was no indication that larvae deposit a clear glistening secretion over the cell surface as they feed, as is reported for *Conanthalictus conanthi* below.

The cell closure on the inside consisted of a concave spiral of approximately three to four distinct coils. The closure material was loose soil that was not waterproof. For all but front cells in series, the outside surface of a cell closure (i.e., partition) was also the rear of the cell in front. Closures of the front cell in a series did not appear to have a special smoothed surface, but such a feature might have been obscured by the fill of the lateral. Females constructing a series obviously constructed the rear cell first, provisioned, oviposited, and then closed the cell, before constructing the cell in front. This was revealed by two nests with single cells at the end of long open side tunnels and by an open cell which contained a small preliminary food sphere in front of a closed cell containing an egg on the completed provisions.

Provisioning and Development: Females carried *Nama* pollen primarily on their hind tibia and femur, although fully laden females had some pollen also on the ventral base of the metasoma and the sides of the propodeum. Transported pollen seemed sticky but not moist. The small (one being 1.5 mm in diameter) spherical pollen-nectar masses found in open cells indicated that early loads of pollen were shaped into small spheres and subsequent loads were added, as was the case at the New Mexico site (and is the case with the higher panurgines, such as the Calliopsini). Complete mealy-moist food masses were completely spherical and 2.15–2.4 mm in diameter (N = 3) [2.0 and 2.5 mm, N = 2]. These spheres were coated with a thin transparent and nonreflective waterproof coating analogous to the transparent waterproof shiny food coatings of the Calliopsini (Andrenidae: Panurginae). Such coatings were not suspected at the New Mexico site and therefore were probably overlooked. Food spheres rested on the lowest part of the cell floor and were not attached to it by any fluid such as nectar or secretions.

One egg was discovered on the top of the food with both of its ends attached to the mass, as was reported to be the case at the New Mexico site. Eggs, 1.20–1.30 mm in length and 0.33 mm in maximum diameter (N = 3), were white and curved and possessed a clear, smooth, shiny chorion. They tapered posteriorly but were otherwise unremarkable in shape (fig. 7). Two preserved eggs in which embryological body segmentation was already evident revealed the embryo to be oriented so that its venter was on the outcurving (upper) side of the egg. In another egg preserved when further developed, the embryo had rotated 180° so that its venter was now on the incurved side, a late embryogenetic reorientation typical of many bees (see Torchio, 1989, and references therein). At the time of hatching the first instar would have been oriented with its venter on the food surface.



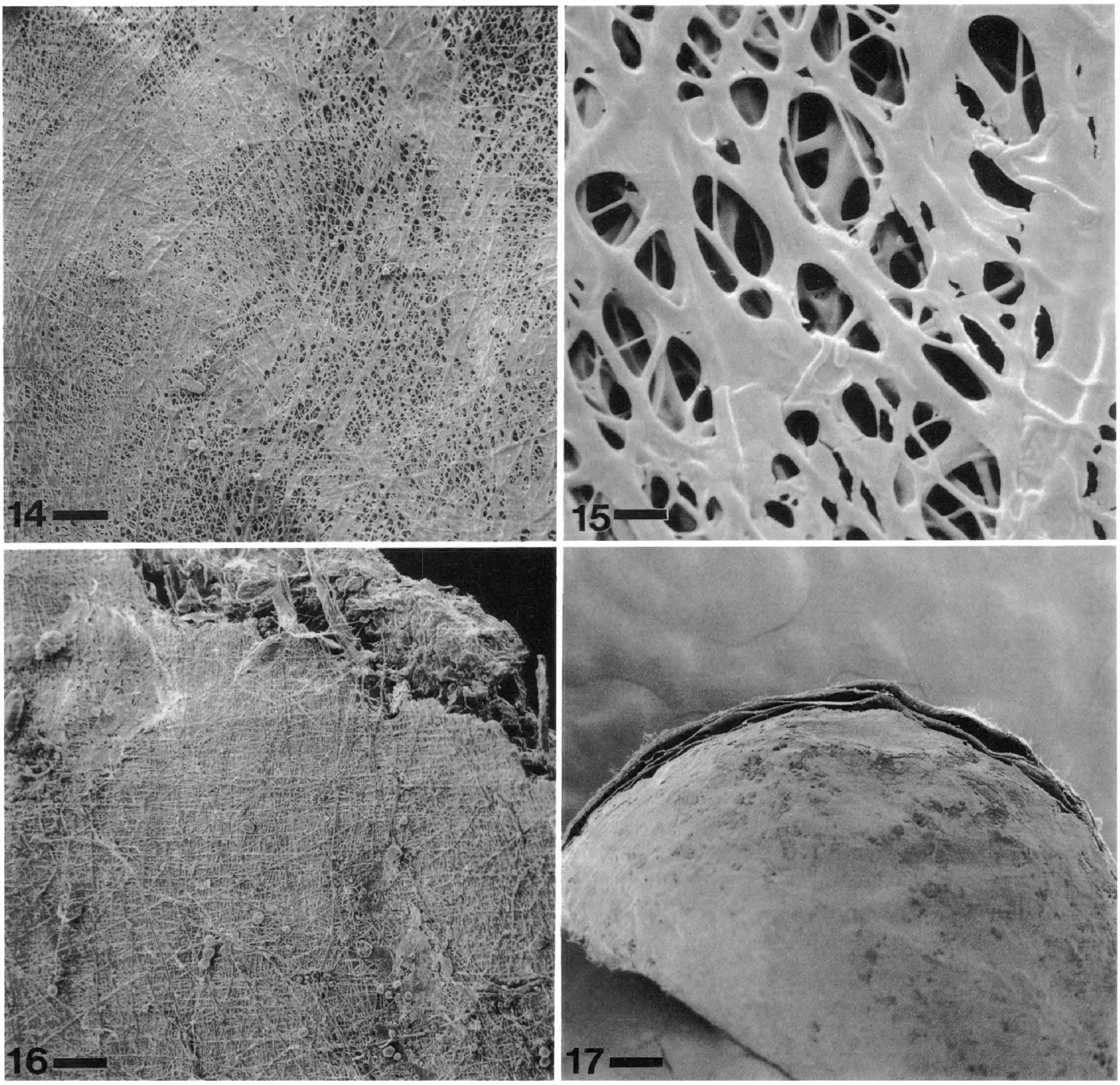
Figs. 12, 13. Cocoons of *Sphecodosoma dicksoni*, front end of cocoons uppermost. **12.** Of single layer of silk, spun by larvae that did not diapause. **13.** Of two layers of silk, spun by larvae that later diapaused. Scale units = 1.0 mm.

Small larvae were uncovered in various positions on the food sphere which became more or less angulate as the larva fed. These facts indicate that larvae crawl on the pollen mass as they graze its surface, as is also suggested by the larva's elongate form (fig. 11). Similar conclusions were reached at the New Mexico site. Large larvae were encountered encircling the pollen masses as the masses became somewhat dumbbell shaped.

Small larvae and those intermediate in size were elongate, and possessed conspicuous rounded (not transverse) paired dorsolateral tubercles on all body segments except the prothorax and abdominal segments IX and X (fig. 11). Middorsal tubercles and subspiracular tubercles, reported for a partly grown larva of *Systropha punjabensis* (Batra and Michener, 1966) were absent. In addition *Sphecodosoma* larvae possessed rounded paired ventrolateral tubercles (presumably the same as the "broad transverse ventral tubercles" of *S. punjabensis*) that were evident on the mesothorax and metathorax and conspicuous on abdominal segments I–VIII. The venter of abdominal segment IX lacked paired tubercles but was strongly produced ventrally. The modification of the venter of abdominal segment IX as well as the paired ventrolateral tubercles of the other body segments probably assist the larva either in crawling or in holding the food mass away from the cell wall while feeding, or both, as is further discussed for *Conanthalictus conanthi* below. Because similar features are found in many (if not all) other rophitines, they should be examined on species with a larger body size so they can be observed more easily. Abdominal segment X was attached dorsally rather than medially to IX giving an appearance of an elevated segment X as seen in lateral view (fig. 11). The function of the somewhat dorsally directed segment X is discussed under *C. conanthi*. Whereas the paired dorsolateral body tubercles, bulging venter of abdominal segment IX, and dorsal position of segment X persist through the last larval instar, the ventrolateral tubercles disappear in the penultimate instar.

As described in the following section, last larval instars possess a strongly projecting labiomaxillary region (fig. 27) (as do the larvae of *Dufourea*); this feature is even more pronounced than in most other cocoon-spinning bee taxa.

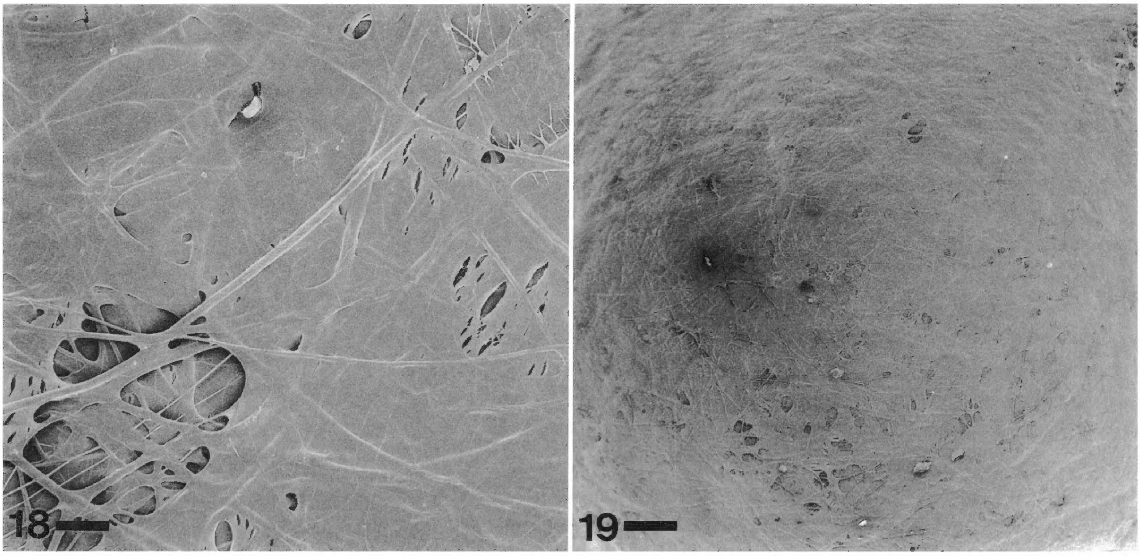
Two types of cocoons were uncovered. One was associated with larvae that molted to the pupal stage without diapausing, the other with larvae that entered diapause and then overwintered. Two cocoons (fig. 12) of the first type from which pink-eyed, active pupae were removed about a week after being collected



Figs. 14–17. Scanning electron micrographs of cocoons of *Sphecodosoma dicksoni*. **14.** Fabric of single-layered cocoon, inner surface; scale = 20 μm. **15.** Close-up of same; scale = 2 μm. **16.** Fabric of double-layered cocoon, outside surface; scale = 20 μm. **17.** Filter area of double-layered cocoon, cross section, showing multiple silk layers; scale = 200 μm.

on April 30–May 1 were externally (and internally) pale tan, almost white. Similar vacated cocoons were uncovered on May 11, after pupae had matured and adults emerged. The fabric of cocoons of this type was very thin (roughly 0.01 mm thick, exclusive of feces), single layered, nearly white, and semiopaque where there was no fecal material. The cocoon (fig. 12) lost its shape when removed from the substrate because the fabric lacked rigidity. Silk strands could not be easily detected even with a stereoscopic microscope except for fine fibers along torn edges. However, when examined under a compound microscope, fine silk strands were quite obvious.

As revealed on scanning micrographs (figs. 14, 15), the fabric was composed of fine silk strands. Some strands were broadly fused to form broad sheetlike areas which were seemingly fibrous but actually had scattered small holes. Other strands fused only where they



Figs. 18, 19. Scanning electron micrographs of cocoons of *Sphecodosoma dicksoni*. **18.** Inner surface of filter area showing nature of inner layer of silk; scale = 200 μm. **19.** Close-up of same, showing opening in cellophanelike material; scale = 20 μm.

crossed one another so that the fabric there was more netlike, with many fenestrations. The fabric was pliable and soft, and scattered sand grains adhered to the outside surface.

Fecal material (vacuolated, flattened pollen exines) as elongate flattened pellets or smears radiated from the rear point of the cocoon and covered only the rear two-thirds. No layer of silk covered the feces inside the cocoon, so that larvae and pupae were in direct contact with the dried fecal material. Where there was no fecal material, the inside surface of the cocoon was smooth and slightly shiny, in general tissue-paperlike. Cocoons of the first type, like cocoons described below, completely filled the cell lumen from the closure to the rear and possessed no outward protuberances (i.e., nipples) at either end, although the front end that fitted the spiral closure conformed externally to the shape of the closure. No special gas exchange area was detected at the front end of this type of cocoon.

The second type of cocoon (figs. 13, 20)[3] (similar in structure to that of *Dufourea novaeangliae*; Eickwort et al. 1986) encountered was a darker tan, more opaque, leathery, and (except for the front end) roughly 0.02 mm thick along the cut edge. On excavation, this type tended to retain its shape because of its rigidity. It consisted of an outer tan mat layer which contained numerous strands of moderately fine silk (fig. 16), some of which were darker than others, visible with a stereoscopic microscope. This layer was spun first and was followed by the deposition of a layer of feces over the entire surface with the apparent exception of a small area at the front of some cocoons. Feces were appressed to the silk as longitudinal ribbons radiating from the front and rear poles of the cocoon. Silk strands could not be detected running through the feces, suggesting that cocoon spinning was not carried out during defecation. This matter, however, needs to be confirmed by observing larvae in the process of defecating. After feces deposition, the larva laid down a thin glistening layer of silk, fibers of which

[3] The type of *Sphecodosoma* cocoon described here closely parallels (excluding size) cocoons of *Dufourea mulleri* which were examined for comparative purposes during this study. The main difference seemed to be that the front (closure) end of the *Dufourea* cocoon was thinner so that at first it did not appear to have a specialized filter area. SEM examination, however, revealed a small multilayered filter, thinner and more restricted than, but otherwise similar to, that of *Sphecodosoma*.

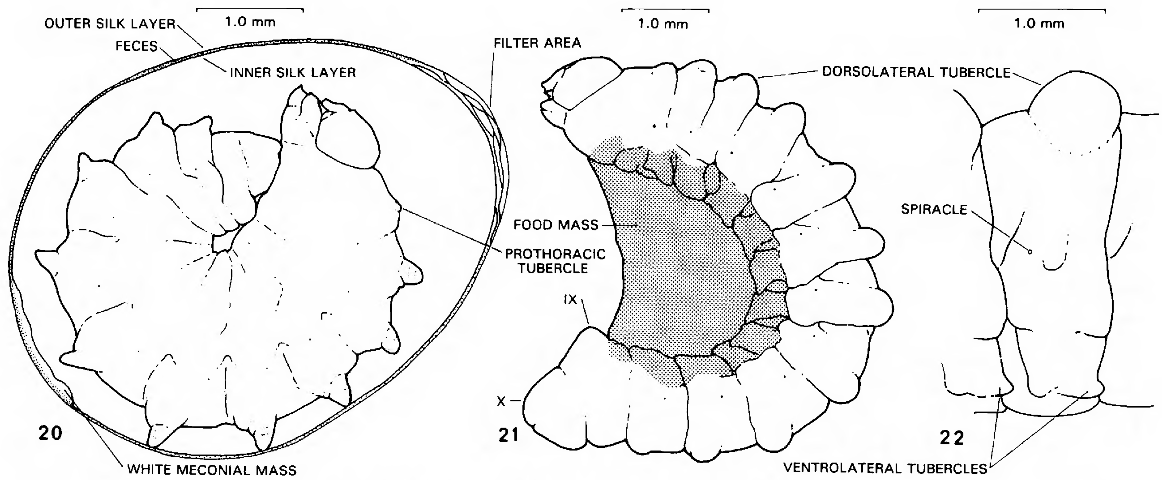


Fig. 20. *Sphecodosoma dicksoni*, diagram of diapausing larva in cocoon, side view. Fig. 21. *Rophites trispinosus*, young intermediate stage larva encircling provision, side view. Fig. 22. *R. trispinosus*, abdominal segment II of older larva, lateral view. Scales as indicated.

were apparently sufficiently moist to fuse with one another, although the fibrous nature of the silk was still evident. This layer was thin, faintly tan and cellophane-like, so that the longitudinal fecal streaks were visible (more so on some cocoons than on others) through it. SEM examination (figs. 17–19) revealed that this material contains relatively few openings.

At the front end of the cocoon, the fabric (figs. 17–20) covering the cell closure consisted of a number of loosely appressed, but not fused, layers of nearly opaque, dense, parchmentlike silk that, combined, were thicker (approximately 0.13 mm or perhaps more) than the fabric of the rest of the cocoon because of the air spaces between layers. The outermost layer was composed of fine silk with many fenestrations, similar to the cocoon fabric of the cocoon described above. Inner sheets appeared to be made from thicker strands that were fused in many places. On some cocoons the central part of this fabric seemed to lack feces and in other cocoons the quantity of feces appeared to be reduced but present. The innermost layer of silk (figs. 18, 19) was cellophanelike, contained few fenestrations, and seemed identical to the rest of the inner surface of the cocoon. Presumably the multilayered front of the cocoon served for gas exchange through the loose soil of the cell closure. The fenestrations in all the layers of fabric apparently permit adequate flow of gas molecules while the cellophane-like baffles may be a filter, excluding parasites.

Two complete or nearly complete cocoons and one incomplete cocoon of this sort were encountered on April 30–May 1. The incomplete one contained a larva that had not yet started to defecate, but the dark outer covering containing visible strands of dark tan silk identified it as the outer layer of an overwintering cocoon. One larva (fig. 20), kept alive in its completed cocoon, became quiescent and assumed a looped shape described below. The larva from the incomplete cocoon was removed from it before defecating. After defecating it spun the glistening fused silk of the inner cocoon layer in a rearing dish in a disorganized fashion, and then it too assumed the looped posture described below. Five completed cocoons of the second type containing looped, diapausing larvae were gathered on May 11.

In each cocoon containing a postdefecating larva, an irregular, lumpy, opaque, whitish meconial mass was plastered to the inside of the rear of the cocoon. It contrasted so strikingly in color and contour with the rest of the inner cocoon surface that at first it seemed to have been deposited after the last layer of silk. In actuality, glistening, nearly transparent silk covered much if not all of it. This indicates that a larva finishes defecating the vacuolated pollen exines and then, while it

is still depositing the inner silk, discharges the white meconial mass.

Although only three cocoons were found in the earlier study in New Mexico, they too represented the two types. As in the present case the three-layered cocoon held a post-defecating larva, and one of the thin cocoons held a larva that soon pupated. These cocoons, preserved in the AMNH, are identical to the ones from the current study.

The looped posture (figs. 20, 25) of quiescent, overwintering larvae was consistent in all cases: the abdomen curved under the front part of the body so that the venter of the terminal two abdominal segments was appressed to the thoracic venter, and the apex of abdominal segment X just reached the base of the labiomaxillary region. Although this posture was not observed while the cocoons were in place in the ground, larvae apparently rest on their dorsa during diapause (fig. 20). This is suggested by the fact that, in several cases, a live quiescent larva had the dorsolateral body tubercles of the mesothorax and first two abdominal segments compressed presumably by the weight of the larva resting on its dorsum. The posture of the hibernating larva of *Dufourea novaeangliae* is different (Eickwort et al., 1986: fig. 4). The looped posture characteristic of *Sphecodosoma dicksoni* is lost when diapausing larvae are preserved in Kahle's solution.

Adult Activity: The information regarding two types of cocoon associated with voltinism suggests that the population is partly univoltine and partly bivoltine (i.e., parsivoltine) as was also hypothesized in the New Mexico study.

Adults were active during the heat of the day, and the numerous males flying about the *Nama* plants indicate that mating normally occurred there. No females attempting to find nests were approached by males. Males and females were not seen to fly *in copulo*.

Parasitism: No cuckoo bees were associated with the nests of this species.

Discussion of Biological Features: The overall agreement between the current study and the one carried out in New Mexico in 1975 is gratifying as are the similarities in the conclusions independently based in each case on somewhat meager data.

Nonetheless, there are differences in cell arrangement (i.e., single or in series), depth, and orientation between the present study and the one based on the New Mexico site that cannot be satisfactorily explained. Nor can the difference in the number of females per nest at the two sites be accounted for. Perhaps examination of sites in other areas, especially those areas geographically intermediate between the two, might give insight into these matters by revealing intermediate conditions. A less likely explanation might be in the different ecological conditions of the two areas (e.g., different substrates, different seasonal rainfall patterns) or for that matter in the different study seasons (i.e., spring versus late summer).

Conanthalictus conanthi

A nest with a single, partly provisioned cell of this species was described by Rozen and McGinley (1976). Data in brackets below refer to the earlier study.

Description of Site: The following investigation was carried out 4 mi east of Willcox, Cochise County, Arizona, where this species has been known to occur for many years. The nesting site (fig. 23) was discovered and studied on May 17, 1992, immediately to the west of an unpaved north-south road. Approximately ten nests were scattered over the horizontal ground among clumps of short grass and the low-growing pollen plant, *Nama hispidum* var. *spathulatum*. The study was continued between August 16, 1992, and September 7, 1992, when the area was again visited. At this time, most of the nests, approximately 15 scattered over an area 20 × 10 m, were immediately to the east of the same unpaved roadway (fig. 24) and the pollen plant was now most abundant on the east shoulder of that road. Although a few of the pollen plants were in bloom on August 16, they appeared to be at maximum bloom at the end of this second study period. During the interval between the May observations and those in the late summer, the *Nama* plants had obviously ceased blooming because of the dry weather during June and early July. The initiation of late summer blossoming was caused by the rains of late July and early August, a common weather pattern for southern Arizona.

Separated only by the width of the roadway, the spring and late summer sites were


23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virtually identical, both on horizontal ground with an uneven surface dominated by clumps of low-growing grass between which were lower barren areas. Cattle trampled the sites from time to time, and their hoofprints created further unevenness in the surface and not uncommonly obliterated nest entrances. Most nests were found in the barren areas. The soil was sandy loam with the following composition: 76% sand, 13% silt, and 11% clay. Calcium and aluminum contents were low. During both periods of observation, moisture content at the cell level was high.

Nest Architecture (figs. 3–6): Active nests could be identified by the tumuli of very fine dry soil at their entrances. The tumuli 1–2 cm in diameter were concentric, eccentric, and acentric depending upon the slope, but all entrance tunnels entered the surface at an oblique angle of 10 to 20° from horizontal. Tunnels normally were open or occasionally briefly blocked by tumuli. Several tunnels as yet without cells were partly soil-filled at the lower levels. Main tunnels, unlined and uniform in diameter throughout, were approximately 1.5 mm (N = 8) in diameter [1.5 mm in 1976 nest] and lacked vestibules. They gradually curved away from the surface over a horizontal distance of 3–4 cm and thereafter generally descended vertically (figs. 3–6). Laterals (about the same diameter as, and similar in appearance to, main tunnels) branched from main tunnels between the depths of 15 and 26 cm (N = 19) [16 cm] and extended 6–17 mm [7 mm] horizontally or slightly downward, ending at cell entrances. Hence, cells tended to be close to the main burrows. All laterals leading to closed cells were soil filled.

Cells were usually arranged singly, but several pairs were found in linear series separated by a short distance (1.25–1.4 mm; N = 2). Their long axes were more or less horizontal or sloped to the rear by as much as 30° from horizontal. Symmetrical around their long axes, cells were elongate ovals with the rear broadly rounded and the front end more narrowly so. Their maximum diameter (2.4–2.6 mm; N = 9) [2.2 mm] was wide relative to the length of the long axis of the cell (3.2–3.8 mm; N = 6) [3.75 mm]. Their entrance was slightly more constricted than the diameter of the lateral.

The nature and deposition of the cell lining in this species appears to be atypical of most ground-nesting bees and is not fully understood because of too few cells and small cell size. Nonreflective (dull) linings on freshly constructed cells immediately absorbed water droplets, indicating that the lining in early stages at least was nonwaterproof. Several cells containing feeding larvae had glistening linings, as if they had been coated with a transparent plastic glue that caused the sand grains of the wall to adhere to one another. The surface was not smooth as is normally the case with cell linings; the sand grains continued to impart a rough texture to the surface. One cell containing a predefecating larva had the entire inner surface of the cell including the cell closure covered by this glistening, gluelike material. The cell containing a postdefecating larva was similar but the feces at the rear of the cell had been discharged over the glistening material. When tested with a water droplet, this lining seemed to retard absorption but was not completely waterproof. These facts suggest that the feeding larva may deposit much of the glistening material as it feeds. Although no feeding larvae were observed doing this, few were found, and they were difficult to examine under field conditions. The labiomaxillary regions of larvae of all ages were so recessed that it seems unlikely the salivary secretion, no matter how fluid, could account for the shiny material. Certainly no fibrous silk was found, and no immature larva of any species of bee is known to produce silk. On the other hand the agile, extensible and retractable, upward-pointed

←

Figs. 23, 24. Nesting sites of *Conanthalictus conanthi*, 4 mi east of Willcox, Cochise Co., Arizona. **23.** Site west of road, studied on May 17, 1992; most nests in center foreground. **24.** Site east of road, studied between August 16 and September 7, 1992; most nests in front of umbrella shadow, center foreground.

abdominal apex raises the possibility that an anal secretion might account for the application of the glistening material.

This matter, of obvious interest, needs further study. A somewhat similar situation was reported for *Colletes* (Torchio et al., 1988, and references therein) and for *Hesperapis larreae* Cockerell (Rozen and McGinley, 1991), suggesting that a broader and more thorough investigation of modifications of cell linings/walls by noncocoon-spinning larvae[4] is warranted. Such a study should not overlook larval anatomical structures possibly associated with applying secretions to cell walls such as may be the case with the abdominal apex of *Conanthalictus* larvae. There are some striking similarities between these larvae (see description of the larva of *C. conanthi* below) and those of some species of *Hesperapis* (Rozen and McGinley, 1974).

Walls of freshly constructed cells were slightly more consolidated than the substrate, and those of cells with glistening material were obviously held together by the reflective cement.

Of the 15 nests excavated, none contained more than three cells, and often the second cell of the nest was much lower than the first. Few cells per nest may be the result of the female's nest construction being disrupted by the cattle in the region, so that, unable to find their nests, females were forced to start new ones. However, some nests contained a mature or nearly mature larva in the upper cell and just an egg or open cell below, a suggestion that the species is slow in nest excavation compared with many other bees. In all cases, older immatures were higher in the nest than younger ones, an indication that nests were progressive.

Provisioning and Development: Females transported dry but apparently sticky pollen on the anterior venter of the metasomata and on their hind tibiae and to some extent on their hind basitarsi, femora, and perhaps even trochanters. A single small pollen-nectar ball in an open cell was only 1.25 mm in diameter and seems to indicate that earlier provisions are shaped into small spheres and that subsequent loads are added to the sphere, as is the case with *Sphecodosoma*. Complete pollen-nectar masses, mealy-moist, and all spherical or nearly so, were 1.45–1.48 mm in diameter (N = 4), and at least one was coated with a nonreflective, transparent material. This material floated from the food surface when the food ball was placed in water.

Eggs (fig. 8) were on top of the pollen-nectar balls in the median sagittal plane of the cell, almost certainly with their rounded anterior end pointed closest toward the cell closure. Strongly curved and whitish, they possessed a transparent, smooth chorion. The anterior end was substantially larger and more rounded than the posterior end, and the egg tapered from just behind the nearly spherical anterior end toward the posterior end.

Young larvae, nearly identical in appearance to those of *Sphecodosoma dicksoni* except lacking prothoracic dorsolateral tubercles, crawled over the food surface as they fed. The food surface was not channeled (as is the case with the food masses of some elongate, crawling anthophorid larvae). The diameter of the food mass decreased as the larva grazed over its surface. A larva moved by detaching and extending the anterior body segments and, after securing the front of the body, by then detaching and contracting the posterior segments. On young larvae the ventrolateral tubercles help establish contact with the food surface, as is the case in *Sphecodosoma* and probably *Rophites* as well. Abdominal segments X pointed dorsally away from the food surface and, when in contact with the cell surface, extended and thus pushed the posterior part of the body forward. That is, it was a dorsally directed pygopod, able to contract and extend, and possibly to apply a secretion to the cell wall as the larva moved over the food ball, as suggested above.

The anatomical mechanism involved with the mobility of the abdominal apex should be studied further, but one component almost certainly is a ventral area between abdominal segments IX and X (fig. 37) that is delimited anteriorly and posteriorly by distinct transverse integumental lines at least on

[4] Stephen et al. (1969) appropriately regarded the larval envelope of *Colletes* as a cocoon. The silk is secreted by the Malpighian tubules through the anus, as is the case for a number of insect groups. For the present study the term noncocoon-spinning larvae refers to bee larvae that do not construct cocoons with salivary silk.

a cleared specimen. This area appears to be part of abdominal segment X because on both male and female larvae the imaginal discs are in their normal position on segment IX defined by the anterior boundary of this specialized area. This area helps elevate the rest of segment X so that it points dorsally. Somewhat similar areas, delimited (e.g., *Xeralictus*; Snelling and Stage, MS) or not (*Sphecodosoma dicksoni*, fig. 28) by transverse integumental lines, are present on other known rophitine larvae causing the terminal segment to point dorsally.

An older larva, mostly grown, was encountered encircling the pollen-nectar mass so as to completely hold the mass away from the cell wall. Presumably at this time the larva no longer moves in relation to the pollen mass. The dorsolateral tubercles on the larva's thorax and abdomen were the points of contact with the cell wall.

A single cell containing a postdefecating larva lacked a cocoon and had the yellow feces applied as a thin layer to the rear one-third of the cell (fig. 10). Blotches of white material appeared on the exposed surface of the feces, representing the final meconial discharge. The greatly recessed labiomaxillary region and obscure palpi on all larvae collected (figs. 35, 36) indicate that this species never spins a cocoon, in contrast to larvae of *Dufourea, Rhophitoides, Rophites, Specodosoma*, and *Systropha*.

ADULT ACTIVITY: Adults were most abundant on flowers during the middle of the day. Mating probably takes place at the flowers judging by the abundance of both sexes there. Males were not seen around nests.

There were two seasons of adult activity at the site, spring and late summer, corresponding with the flowering of *Nama*. Because mature larvae and pupae were not uncovered from nests on May 17, it is unknown how individuals aestivate between spring and late summer. It does seem clear, however, that they are inactive during this time because of the absence of flowering food plants. Two postdefecating larvae collected and preserved in early September had developed pupal tissue, an indication that they would have matured the same season. Other known rophitines (*Dufourea, Rhophitoides, Rophites, Sphecodosoma, Systropha* and apparently *Xeralictus*) hibernate as mature larvae (as do most bees) so that *Conanthalictus* may pass the winter as quiescent postdefecating larvae. If this is true, then *C. conanthi* has an annual bimodal adult activity pattern in favorable years at this locality and seems to be multivoltine so long as the food source is available.

PARASITISM: No cuckoo bees were associated with the site, either in the spring or late summer. The single postdefecating larva from a nest containing but a single cell had an elongate white egg (fig. 40) attached to the front right side of its body. The egg, presumably that of a mutillid, had a spiculated chorion and one end more rounded than the other. The main burrow of this nest (fig. 5), unlike burrows of other nests, was filled with soil in many places, presumably the result of the parasite's activity.

Rophites trispinosus

I was shown the nesting site of this species by Professor J. de Beaumont at Vercorin, Valais, Switzerland, elevation 1340 m, on July 4, 1964, where nests occurred along a barren, trodden foot path. Although I made no notes on the excavations, the following is derived from larvae and food masses preserved at that time.

PROVISIONING AND DEVELOPMENT: A single food mass, spherical and 4.1 mm in diameter, was preserved in Kahle's solution. No waterproof coating was visible, although a coating may have dissolved in the preservative. A curved egg (fig. 9), 2.4 mm long and 0.6 mm in maximum diameter, possessed a reticulated chorion and was rounded at the anterior end and considerably more pointed at the posterior end. The embryo within was oriented with its venter against the outcurved side. An intermediate-stage larva (fig. 21) encircled another food mass, suggesting that it gripped the mass tightly while it fed on it.

Intermediate-stage larvae (fig. 21) as well as a large larva (fig. 22) with salivary lips (probably a young last-stage larva, described in the section of mature larvae, below) possessed paired dorsolateral body tubercles. As in other rophitines (except for *Conanthalictus conanthi*), the prothoracic tubercles were much smaller than the others, but the paired dorsal tubercles of abdominal segment VIII

were scarcely if at all evident. Middorsal tubercles (reported for *Systropha* by Batra and Michener, 1966) were absent, but subspiracular protrusions (tubercles?) were evident at least on a medium-size larva. Intermediate larvae of all sizes (figs. 21, 22) (including the specimen with protruding salivary lips) possessed a pair of small, posteriorly directed, ventrolateral tubercles toward the posterior margins of the mesothorax, metathorax, and abdominal segments I–VII. These tubercles were quite distinct, much like those of *C. conanthi*, and not as large and vague as those of *S. dicksoni*. The tubercles as well as the strongly protuberant venter of abdominal segment IX suggest that these structures probably function in the same way as do their homologs in *C. conanthi* and *S. dicksoni*. The protruding (but very narrow) salivary lips and a labium divided into a prementum and postmentum found on the specimen (figs. 41, 42) that was presumably an early last instar indicates that this species spins a cocoon.

PARASITISM: Adults of the cuckoo bee *Biastes emarginatus* (Schenck) (Nomadinae: Biastini) were captured as they flew over the path, leaving little doubt that they parasitized the nests of this host. However, it was not until I examined preserved larvae in connection with this paper that I realized that an intermediate-stage larva of this cleptoparasite had been recovered. The anterior end of the specimen had been covered with pollen, its midsection somewhat damaged and distorted, and the protruding venter of abdominal segment IX and dorsolateral body tubercles were surprisingly similar to those of the host. This is apparently the first association of this cleptoparasite with *Rophites trispinosus* although it has been associated with *R. quinquespinosus* Spinola (Stöckhert, 1922).

The similarities between this specimen and the mature larva of the related *Neopasites* (Biastini) (Rozen, 1966) are striking. Those italicized below are characteristic of mature larvae of the Nomadinae (sensu Roig-Alsina, 1991); those in boldface are probably synapomorphies of the Biastini and in some cases Neolarrini. **Head capsule with antennal papilla small but projecting; labrum very short, somewhat recessed behind frontoclypeal area (as seen in lateral view) and bearing pair of labral tubercles. Mandibles apically thin, sharp-pointed,** and *so short that their apices do not reach one another. Labiomaxillary region greatly fused.* Larva unusually elongate; most body segments possessing low, rounded dorsolateral tubercles. **Posterior part of abdomen** (quite similar to that of its host) **with venter of abdominal segment IX protruding; abdominal segment X somewhat dorsal in attachment to IX.**

PROFILE OF THE BIOLOGY OF THE ROPHITINAE

Sufficient information is on hand to present an overview of the biological features (except for pollination biology) of the Rophitinae, as has been done for some other higher taxa (Rozen, 1977, 1984a, 1984b, 1989). This information comes from the following accounts:

Conanthalictus conanthi (Cockerell)
 Rozen and McGinley (1976); present study
Dufourea malacothricis Timberlake
 Torchio et al. (1967)
D. mulleri (Cockerell)
 Torchio et al. (1967)
D. novaeangliae (Robertson)
 Kukuk et al. (1985); Eickwort et al. (1986)
D. pulchricornis (Cockerell)
 Torchio et al. (1967)
D. trochantera Bohart
 Torchio et al. (1967)
Rhophitoides canus (Eversmann)
 Enslin (1921); Malyshev (1925b)
Rophites hartmanni Friese
 Malyshev (1925b, 1935)
R. quinquespinosus Spinola
 Stöckhert (1922)
Sphecodosoma dicksoni (Timberlake)
 Rozen and McGinley (1976); present study
Systropha curvicornis (Scopoli)
 Malyshev (1925a)
S. planidens Geraud
 Malyshev (1925a)
S. punjabensis Batra and Michener
 Batra and Michener (1966)
Xeralictus timberlakei Cockerell
 Snelling and Stage, MS

The profile is tentative because the nesting biologies of many genera (*Michenerula, Micralictoides, Morawitzella, Morawitzia, Penapis, Protodufourea, Systrophidia*, and *Trilia*) have yet to be examined, and even the most detailed published accounts are still incomplete. Hopefully, the profile will encourage studies of other genera and provide comparative points of reference. Certain similarities

in the biologies seem distinctive for the subfamily and are italicized.

GENERAL: Subfamilial distribution (Michener, 1979) primarily Holarctic but reaching southern Africa and southeast Asia; one genus (*Penapis*) in South America; no representation in Australia; most abundant in xeric regions. Body size minute to moderate.

NESTING: All species ground nesting, solitary, mostly noncommunal, often apparently nesting in loose aggregations; none cleptoparasitic. Nesting surface horizontal, sloping, and even vertical. Substrate texture apparently variable. Nests shallow (< 10 cm deep) to moderately deep (maximum depth recorded 33 cm), apparently always progressive; preexisting cavities and old nests not used. *Tumuli present, usually eccentric or acentric and bilaterally symmetrical*; turrets absent. Nest consisting of single, open (at least above) main tunnel and short to moderately short subhorizontal laterals that are soil-filled when completed. *Main tunnels of many species entering ground at oblique angle to horizontal, meandering considerably in upper part, and descending more vertically and with less meandering in lower part*; main tunnels without vestibules, blind laterals, or blind terminal burrows. Nests with a number of cells; cells arranged singly and also commonly in linear series, but not in clusters; cells in series separated by only width of closure; cells ovoid, apparently tending to be symmetrical around long axis and short relative to maximum diameter; cell orientation horizontal, subhorizontal, or tilted to rear by as much as 40 or even 70° from horizontal. *Cell lining dull, more or less water absorbent*; cell walls not obviously soil lined. Cell closure more or less concave spiral of three to four coils.

PROVISIONING: Pollen transported primarily on hind femur, tibia, and basitarsus and in many taxa also on sides of propodeum, and in *Systropha*, *Systrophidia*, and others also abundantly on sides and undersurface of metasoma. *Early pollen-nectar loads shaped into small sphere; completed provisions spherical;* provisions of some species with waterproof or semiwaterproof, presumably secreted, transparent coating, but this coating apparently absent in other species; provisions not attached by liquid to cell floor.

DEVELOPMENT: Eggs apparently usually strongly curved, placed on top of food mass; *young larvae elongate, capable of crawling as they feed so that pollen-nectar mass reduced in size but remaining spherical*; older larvae grasping food mass while feeding on it and holding it away from cell wall; food mass now looses spherical shape. Cocoons of salivary silk constructed except in *Conanthalicus* and presumably in *Xeralictus*, completely filling cell lumen; cocoon fabric (except at front end) thin, normally consisting of two layers of silk (except in case of nonhibernating larva of *Sphecodosoma dicksoni*) between which there is layer of feces; defecation commencing after all food consumed and outer layer of cocoon produced; feces applied to rear of cocoon and often extending only part way to front of cocoon; inner layer of silk covering feces; front of cocoons often with specialized thicker fabric consisting of several silk layers separated by air spaces, without macropyle (Rozen and Jacobson, 1980).

ADULT ACTIVITY: Bees diurnal, probably flying primarily during middle of day; most species probably univoltine, but some parsivoltine, and others multivoltine. Bees overwintering as quiescent larvae in cocoons (unknown for *Conanthalictus*). Many species oligolectic (Hurd, 1979).

CLEPTOPARASITIC BEES: Among Biastini, *Neopasites* definitely associated with some species of *Dufourea* (Hurd, 1979); *Biastes* with *Rophites*, *Systropha*, and *Dufourea* (Popov, 1933); and *Rhopalolemma* almost certainly with *Protodufourea* (Eickwort, personal commun.). In Townsendiellini, *Townsendiella* suggested as cleptoparasite of *Conanthalictus*, but this yet to be confirmed.

MATURE LARVAE OF THE ROPHITINAE

The following is based on available specimens of *Conanthalictus, Dufourea, Sphecodosoma, Xeralictus,* and an immature specimen of *Rophites*. It also takes into account information from the literature on *Dufourea mulleri* (McGinley, 1981, 1987); *D. novaeangliae* (Eickwort et al., 1986); *Systropha punjabensis* (Batra and Michener, 1966); and *Xeralictus timberlakei* (Snelling and Stage, MS).

DIAGNOSTIC DESCRIPTION: Mature larvae of the Rophitinae can be recognized by the following characters (features in boldface

should be particularly convenient to use): Clypeus and labrum usually short (except for *Xeralictus* and perhaps *Rophites*), usually without obvious paired tubercles but these present in *Rophites* (and apparently *Rhophitoides* [Enslin, 1921: fig. 1] and *Systropha* [Batra and Michener, 1966]); hypopharyngeal groove absent (*Conanthalictus, Dufourea, Sphecodosoma*), present laterally (as indentation along articulating arms of stipites) but not medially (*Rophites*), or complete (only in *Xeralictus*). Intrasegmental lines (figs. 25, 32, 37) not evident at least dorsally (weakly developed in *Xeralictus*); **dorsolateral body tubercles conical (i.e., not transverse), present on most body segments; those of pronotum absent *(Conanthalictus)* or noticeably smaller (all others) than those of following segments;**[5] labiomaxillary region more (fig. 27) or less (fig. 42) produced except greatly recessed in *Conanthalictus* (fig. 35); salivary opening transverse, with projecting narrow lips (figs. 28, 41, 42) except lips absent in *Conanthalictus* (figs. 35, 36); **abdominal segment IX (figs. 35, 26, 29) more or less produced ventrally; abdominal segment X (figs. 25, 26, 39) dorsal in attachment to IX and directed somewhat dorsally.**

Some of the characters used before (Eickwort et al. 1986; McGinley, 1987) to differentiate the larvae of the Rophitinae from other taxa are no longer as useful. For example not all rophitines have strongly projecting labiomaxillary regions and transverse, projecting salivary lips (*Conanthalictus*), and some rophitines (*Rophites, Xeralictus*) have a large seta-bearing tubercle on the outer surface of the mandible.

[5] Eickwort et al. (1986) stated that the dorsolateral prothoracic tubercles of the then-known rophitines were "only slightly lower than the other thoracic tubercles" rather than "markedly reduced" as reported by Rozen and McGinley (1976). Through the kindness of George C. Eickwort, I have been able to examine the mature larva of *Dufourea novaeangliae* and agree that the prothoracic tubercles, though smaller than the mesothoracic ones, are not as greatly reduced in relation to the other dorsolateral body tubercles as those of *Dufourea mulleri*. Nonetheless, prothoracic tubercles smaller than those of the meso- and metathorax (or absent) impart a characteristic appearance to all larval rophitines that I have seen.

Key to the Mature Larvae

1. Labiomaxillary region (figs. 29, 42) not recessed; labium divided into prementum and postmentum; salivary lips (figs. 29, 42) present; maxillary and labial palpi (figs. 29, 42) as long as or longer than their basal diameters; prothoracic dorsolateral tubercles (figs. 25, 26) present but smaller than those of following segments 2
– Labiomaxillary region (fig. 35) greatly recessed; labium (fig. 34) undivided; salivary lips absent (fig. 35); maxillary palpi (fig. 36) scarcely evident; labial palpi (fig. 36) undeveloped except for sensilla; prothoracic dorsolateral tubercles absent, following tubercles well developed (fig. 37) .... *Conanthalictus conanthi*

2(1). Labiomaxillary region not extending beyond labrum in lateral view (fig. 42); outer surface of mandible with large seta-bearing tubercle (figs. 43, 45); articulating arm of stipital sclerite conspicuous (fig. 41) .. 3
– Labiomaxillary region strongly projecting beyond labrum in lateral view (fig. 27); outer surface of mandible with seta-bearing tubercles very small, inconspicuous (figs. 29, 31) or moderately small (*Dufourea*, Eickwort et al., 1986: fig. 14); articulating arm of stipital sclerite inconspicuous (fig. 28) 4

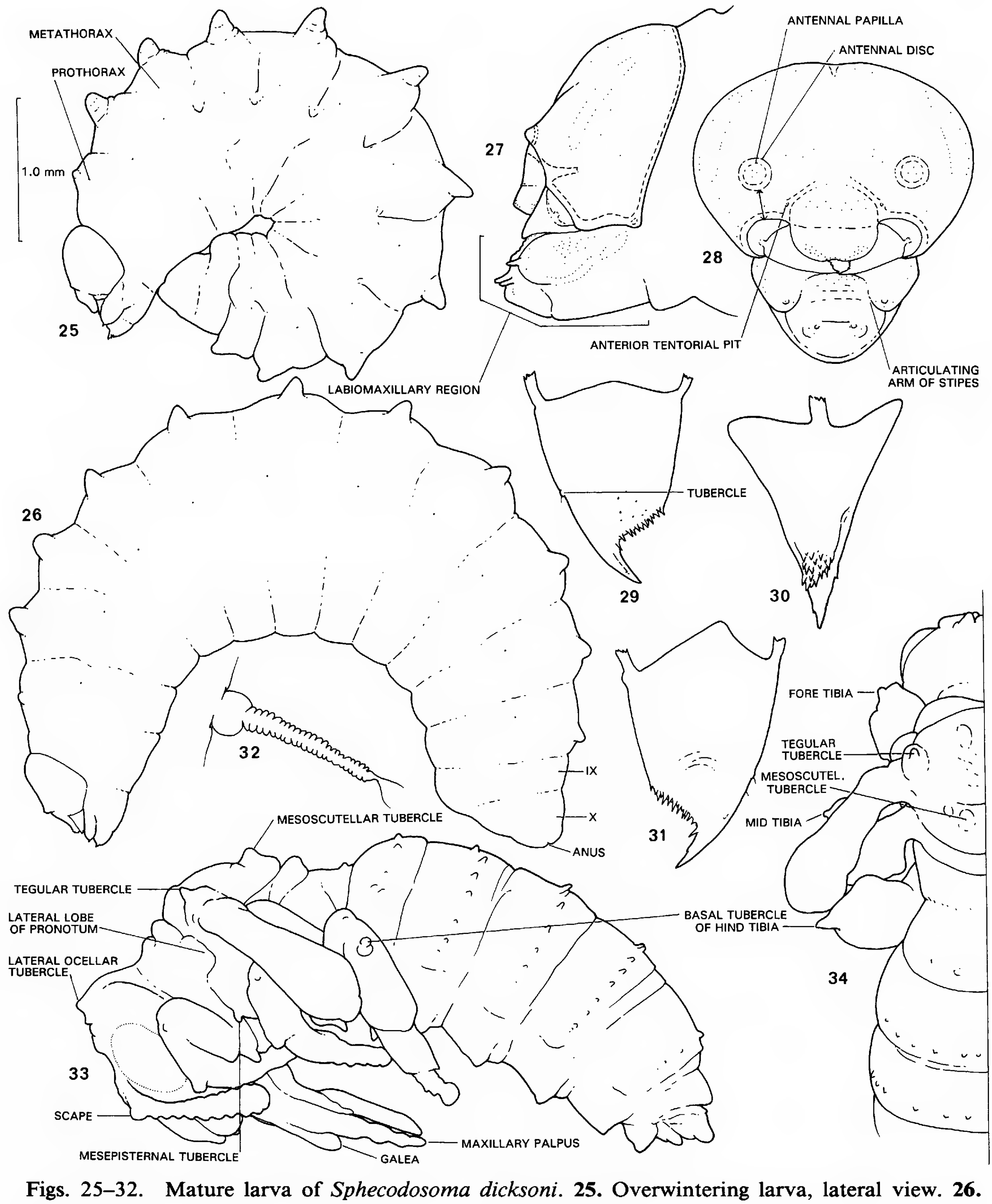
3(2). Labral tubercles absent; antennal papilla shallow, projecting less than half its diameter .... *Xeralictus timberlakei*
– Paired labral tubercles (fig. 42) well developed; antennal papilla small but projecting, about as long as basal diameter (fig. 42) .... *Rophites trispinosus*

4(2). Antennal disc (McGinley, 1987: fig. 27.187a) on cleared head capsule moderate in size, so that distance between disc and upper edge of mandibular corium (as measured by arrow in fig. 28) is 1.5 to 2 times disc diameter; subatrium of normal length, of less than 13 chambers .... *Dufourea mulleri* and *D. novaeangliae*
– Antennal disc (fig. 28) large, so that distance between disc and upper edge of mandibular corium is less than 1.5 times disc diameter; subatrium (fig. 32) abnormally long, of 15 or more chambers .... *Sphecodosoma dicksoni*

Sphecodosoma dicksoni

Figures 28–32

The format and terminology used here are those proposed by Rozen and Michener (1988).



Figs. 25–32. Mature larva of *Sphecodosoma dicksoni*. **25.** Overwintering larva, lateral view. **26.** Predefecating larva, lateral view. **27, 28.** Head, lateral and frontal views, respectively. **29-31.** Right mandible, dorsal, adoral, and ventral views, respectively. **32.** Spiracle, side view. Figs. 33 and 34. Pupa of *Sphecodosoma dicksoni*, lateral and dorsal (left half) views, respectively. Scale refers to figures 26, 27, 33, and 34.

DIAGNOSIS: At present the only known characters (in boldface) by which mature larvae of *Sphecodosoma* can be distinguished from those of other Rophitinae are the large antennal discs and papillae and the very elongate, multichambered subatrium. *Rophites* also has a long, multichambered subatrium but can be recognized by its very small antennal papilla relative to the moderately large disc (fig. 41).

HEAD (figs. 27, 28): Integument of head capsule with scattered sensilla that are small and not obviously setiform. Integument unpigmented except for mandibular apices, mandibular articulations, and, in postdefecating larvae, salivary lips.

Head size (figs. 25, 26) small compared to body size; head capsule distinctly wider than length measured from top of vertex to lower clypeal margin in frontal view. Tentorium well developed, possessing well developed dorsal arms; anterior tentorial pits normal in position, not immediately adjacent to anterior mandibular articulations; posterior tentorial pits in normal position at junction of posterior margin of head and hypostomal ridges; postoccipital ridge (i.e., posterior thickening of head capsule) moderately developed, scarcely curving forward medially as seen in dorsal view; posterior margin of head normal in position; median longitudinal thickening of head capsule absent except for faint thickening of integument at very top; hypostomal ridge strongly developed, without ramus, of moderate length, forming approximately 90° angle with posterior margin as seen in lateral view (fig. 27); pleurostomal ridge only moderately developed; epistomal ridge moderately developed, extending almost to midline on front of head (fig. 28); epistomal depression inconspicuous. Parietal bands evident. Antennal prominence moderately weak (fig. 27); **antennal disc large (fig. 28); antennal papilla large (fig. 28),** bearing three sensilla. Vertex evenly rounded as seen from side (fig. 27), without unusual projections; clypeus of moderate width, short so that clypeolabral suture almost in line with anterior mandibular articulations as seen in frontal view (fig. 28); frontoclypeal area in lateral view (fig. 27) scarcely projecting and not produced beyond labrum. Labrum in lateral view projecting only slightly beyond clypeus; labral sclerite not evident; labral tubercles (fig. 27) very weak, inconspicuous, but present, too vague to determine whether arising from labral disc or labral apex; lateral areas bearing a few scattered spicules; epipharyngeal surface nonspiculate except laterally.

Mandible (figs. 29–31) moderately robust at base tapering to simple, slender apex; dorsal mandibular surface with a few small, sharp-pointed spicules; outer surface of mandible with seta-bearing tubercle small, not pronounced; dorsal adoral surface with numerous large sharp-pointed teeth in vicinity of cusp; dorsal apical edge bearing one or two teeth; ventral apical edge apparently either nondentate or bearing one or two teeth; apical concavity weakly developed, apparently represented by shallow groove extending from apex along ventral surface; this area nonspiculate. Labiomaxillary region (fig. 27) greatly produced. Maxillary apex not produced mesally; sclerotized cardo and stipes unpigmented, difficult to see but represented by thickened integument best seen on cleared specimen; articulating arm of stipital sclerite difficult to see but present in position shown (fig. 28); galea not produced as low swelling but perhaps represented by sensillum mesad of maxillary palpus; maxillary palpus elongate, longer than basal diameter. Labium divided into prementum and postmentum; premental sclerite unpigmented; labial palpus equal in size to maxillary palpus. Salivary opening a moderately narrow transverse slit borne of projecting, well-developed lips. Hypopharynx a vaguely transversely grooved surface bearing spicules medially, gently curved but not strongly bulging; hypopharyngeal groove not developed so that hypopharyngeal surface grading into dorsal labial surface.

BODY: Integument without setae but dorsolateral tubercles with small sensilla; ventral areas of most body segments with small evenly spaced spicules; dorsal integument of abdominal segments VII–X with fine transverse linear asperities that become increasingly pronounced toward abdominal apex; dorsolateral tubercles microscopically irregularly roughened compared with rather smooth integument elsewhere. Body form (figs. 25, 26) moderately robust, not greatly elongate (al-

though early instars quite elongate); intersegmental lines weakly incised; intrasegmental lines (figs. 25, 26) not evident; paired dorsolateral body tubercles conspicuous on mesothorax, metathorax, and abdominal segments I–VIII, comparatively reduced in size on prothorax, absent on abdominal segment IX, X; tubercles conical rather than transverse; other tubercles absent on mature larva (see section on biology for other instars); venter of abdominal segment IX produced; X attached dorsally to IX; apex of X without ridges or other modifications; anus dorsal in position at apex of X, as seen in lateral view (figs. 25, 26). **Spiracles (figs. 25, 26, 32) extremely small** and inconspicuous; thoracic spiracles slightly larger than others; spiracles without sclerites, not on tubercles; peritreme apparently present; atrium perhaps projecting slightly above body wall, with distinct rim, globose; atrial wall smooth; primary tracheal opening with collar; **subatrium (fig. 32) extremely long, consisting of many chambers (at least 20 on thoracic spiracles but fewer on abdominal spiracles).** Male with distinct but small cuticular invagination ventrally on midline of abdominal segment IX near its posterior margin; female characters unknown beyond the absence of male character stated above.

MATERIAL STUDIED: 2 postdefecating, 4 predefecating larvae 18 mi west of Blythe, Riverside Co., California, April 30, May 1, 11, 1992 (J. G. and B. L. Rozen).

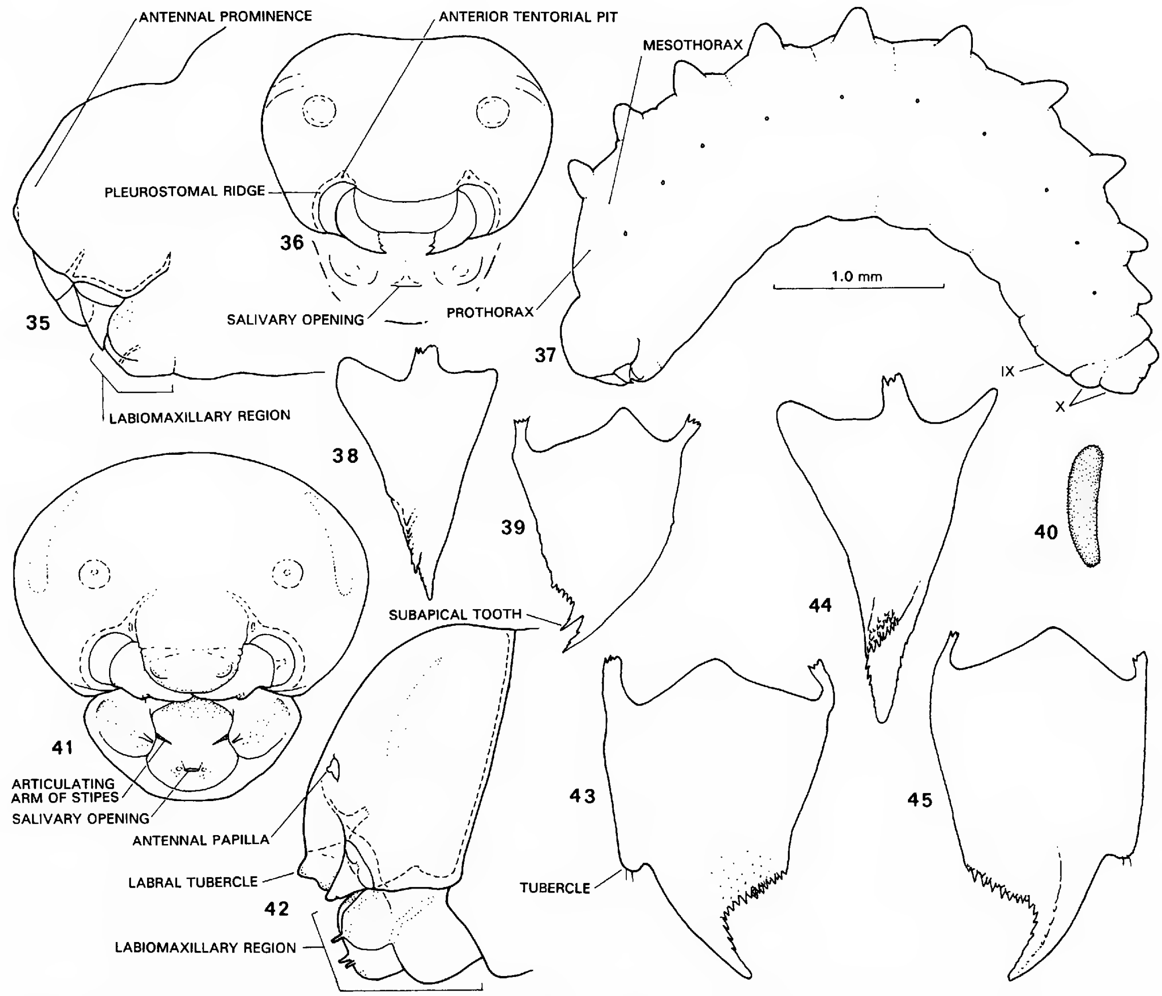
Conanthalictus conanthi
Figures 35–39

DIAGNOSIS: The numerous characters presented in the following description will easily separate this species from other known larvae in the subfamily. Those that are especially diagnostic are in boldface.

HEAD (figs. 35, 36): As described for *Sphecodosoma dicksoni* except for following: **Sensilla of head capsule so small that those of antennae, palpi, and parietals are scarcely if at all visible under high stereoscopic magnification.** Integument unpigmented except for mandibular apices; anterior and posterior tentorial arms present but rest of tentorium absent perhaps because specimen approaching ecdysis; **anterior tentorial pit (fig. 36) laterad of anterior mandibular articulation so actually occurring on (or just above) pleurostomal ridge; postoccipital ridge (posterior thickening of head capsule) (fig. 35) absent** although posterior boundary of capsule delimited by constriction; median longitudinal thickening of head capsule absent; hypostomal ridge moderately developed; **epistomal ridge (fig. 36) absent;** epistomal depression absent. Parietal bands not evident. **Antennal prominence (fig. 35) large, globose, occupying much of anterolateral area of parietal;** antennal disc of moderate size; antennal papillae not fully differentiated from disc, projecting only slightly, bearing unknown number of sensilla. Clypeus presumably short as in *Sphecodosoma* but upper boundary not demarked by epistomal ridge; clypeolabral suture almost in line with anterior mandibular articulations; frontoclypeal area in lateral view even less projecting than in *Sphecodosoma*, appearing recessed because of large antennal prominences. Labrum (fig. 35) not projecting as far as clypeus in lateral view; labral tubercles virtually absent; labrum and epipharynx apparently not spiculate.

Mandible (figs. 38, 39) with conspicuous subapical tooth; dorsal surface without spicules; outer surface with only minute tubercle; dorsal adoral surface without teeth except for conspicuous sharp-pointed teeth that extend along dorsal apical edge; ventral apical edge without teeth. **Labiomaxillary region (fig. 35) greatly recessed.** Cardo, stipes, articulate arm of stipital sclerite not evident; maxillary palpus scarcely evident, much shorter than basal diameter. **Labium** not divided into prementum and postmentum, **very short**, its posterior margin in line with posterior constriction of head capsule as seen in figure 35; **labial palpus not evident** except perhaps for vague sensilla. **Salivary lips absent; opening of salivary duct (fig. 36) a transverse slit.** Hypopharynx nonspiculate, apparently not grooved; hypopharyngeal groove absent.

BODY: Dorsolateral tubercles with apices perhaps slightly roughened but sensilla not evident; some areas of body weakly spiculate but without fine transverse linear asperities. Body form (fig. 37) moderately slender; **paired prothoracic dorsolateral tubercles absent;** abdominal segment IX with small paired dorsolateral tubercles; venter of abdominal seg-



Figs. 35–39. Postdefecating larva of *Conanthalictus conanthi*. **35, 36.** Head, lateral and frontal views, respectively. **37.** Entire larva, lateral view. **38, 39.** Right mandible, adoral and ventral views, respectively. Fig. 40. Egg of parasite (probably a mutillid) found attached to postdefecating larva. Figs. 41–45. Probable early last larval instar of *Rophites trispinosus*. **41, 42.** Head, frontal and lateral views, respectively. **43-45.** Right mandible, dorsal, adoral, ventral views, respectively. Scale refers to figures 37 and 40.

ment IX weakly produced but appearing pronounced because of small, dorsally positioned abdominal segment X; X connected to IX ventrally by anterior extension which permits tip of abdomen to be directed dorsally (fig. 37). Spiracles moderately small but appearing obscure because of lack of pigmentation; spiracles subequal in size; atrial wall perhaps faintly ringed; subatrium normal in length, consisting of 8 or 9 chambers. Male with distinct but small cuticular invagination posteriorly on ventral midline of abdominal segment IX as in *Sphecodosoma*; female with paired white, opaque, imaginal discs visible through ventral integument of abdominal segments VII, VIII, and IX; those of IX nearly contiguous.

Material Studied: Two postdefecating larvae, 1 predefecating larva, and 2 nearly mature larvae, 4 mi east of Willcox, Cochise Co., Arizona, September 1–5, 1992 (J. G. and B. L. Rozen).

Remarks: Features of the head of the larva are remarkably different from those of the other rophitines, but at the same time such important synapomorphies as the reduction

(absence) of paired prothoracic dorsolateral tubercles, short labrum and clypeus, and modifications of the abdominal apex demonstrate its affinities to other members of the subfamily. It seems likely that many of the head modifications (reduction of labiomaxillary regions, reduction in size of palpi, loss of salivary lips, and perhaps the loss of the epistomal suture) are related to the fact that this species does not spin a cocoon. Such reductions are found in other noncocoon-spinning bee larvae. However, other features (reduction in size of head sensilla, globose antennal prominences, and loss of postoccipital ridge) are more difficult to explain. The apparent position of the anterior tentorial pits on the pleurostomal ridge is unusual. Since the pits are actually slightly above this ridge (fig. 36), the brief ridges connecting them to the pleurostomal ridges are probably the lateral remnants of the epistomal ridge.

Rophites trispinosus

Figures 22, 41–45

The following information is based on a single larva (also discussed in the section on nesting biology) that is poorly preserved, not fully mature, and probably teneral. The following features suggest that it may be the last instar: well developed salivary lips, long slender palpi, sclerotized maxillary sclerites, and spiracular development. However, the labiomaxillary region (fig. 42) projects only moderately and the ventrolateral tubercles are well developed (such tubercles are not evident in last-stage larvae of *Sphecodosoma dicksoni*). Whatever its stage, it does provide enough information about the last stage for the following abbreviated description.

DIAGNOSIS: This larva can be separated from those of other known rophitines (with the possible exception of *Systropha*, Batra and Michener, 1966) in that the labrum bears a pair of distinct, apically rounded labral tubercles. An illustration of the mature larva of *Rhophitoides canus* (Enslin, 1921: fig. 1) suggests that it also has paired labral tubercles.

HEAD (fig. 41, 42): As described for *Sphecodosoma dicksoni* except for following:

Only mandibular apices faintly pigmented (presumably because specimen teneral). Epistomal depression absent. Antennal disc moderate in size; **antennal papilla small but strongly projecting, about as long as basal diameter;** clypeus of moderate length; position of clypeolabral suture indefinite relative to anterior mandibular articulations. **Labrum in lateral view extending beyond clypeus because of pair of rounded labral tubercles that arise from labral disc;** lateral areas of labrum spiculate; epipharyngeal surface spiculate.

Mandible (figs. 34–45) with dorsal surface more densely spiculate that of *Sphecodosoma dicksoni*; **outer surface of mandible (figs. 43, 45) with pronounced seta-bearing tubercle;** dorsal apical edge bearing numerous small teeth and irregularities; ventral apical edge with small teeth and irregularities. Labiomaxillary region not greatly produced. **Maxilla with articulating arm of stipital sclerite (fig. 41) long, well developed**; maxillary palpus elongate, even more so than that of *S. dicksoni*. Labial palpus like maxillary palpus. Salivary lips (figs. 41, 42) well developed, projecting but very narrow. Hypopharynx more strongly curved than that of *S. dicksoni*; hypopharyngeal groove evident laterally as indentation along articulating arms of stipital sclerite.

BODY: As described for *Sphecodosoma dicksoni* except for following: Integumental spicules and sculpturings unknown because larva poorly preserved and teneral. Body form of mature larva unknown (early instars elongate); intersegmental and intrasegmental lines impossible to evaluate because larva not fully fed; paired, rounded dorsolateral body tubercles large and very conspicuous on mesothorax, metathorax, and abdominal segments I–VII; prothoracic tubercles smaller than following ones; abdominal segment VII apparently with small dorsolateral tubercles; size of all dorsolateral tubercles of little comparative value because specimen immature (hence body not drawn in lateral view); ventrolateral tubercles present on many segments (fig. 22) (but these tubercles are probably absent on fully fed larva). Spiracles small; sizes relative to one another unknown; subatrium long, consisting of more than 15 chambers (i.e., like that of *S. dicksoni*, fig. 32). Male with distinct cuticular invagination on venter of abdominal segment IX (as in *S. dicksoni*); female sex characters unknown.

MATERIAL STUDIED: 1 immature, possibly last instar, Vercorin, Switzerland, July 4, 1964 (J. G. Rozen).

PUPA OF *SPHECODOSOMA DICKSONI*

Figures 33, 34

DIAGNOSIS: Because no other pupa of this subfamily has been described (although that of *Rhophitoides canus* was pictured by Enslin, 1921), distinguishing features separating this species from related taxa cannot be given. No doubt the size, shape, and distribution of pupal tubercles (in contrast to tubercles that cover developing adult features) will be diagnostic. The extremely elongate maxillary palpi relative to the short galeae (reflecting the sizes of the adult structures) (fig. 33) may be important in recognizing pupae of many Rophitinae.

HEAD: Integument possibly spiculate but difficult to see, some areas with indistinct irregularities, but without setae. Scape with several integumental irregularities on outer surface and with large rounded apical tubercle; pedicel and flagellum without tubercles. Vertex with lateral ocellar tubercle on each side arising from irregular, raised base; median ocellar tubercle small; genal tubercle absent; frons with lumpy elevation on each side; clypeus without tubercles; labrum unmodified. Mandible very strongly swollen subapically but without tubercles; other mouthparts without tubercles.

MESOSOMA: Integument finely, evenly spiculate in some places; setae absent. Lateral lobe of pronotum swollen but without tubercle; posterior margin of pronotum with transverse swelling on each side; mesepisternum with small but distinct rounded tubercle behind foretrochanter (fig. 33); mesoscutum with low mound on each side near anterior margin; axilla with low mound; mesoscutellum with moderate tubercle on each side; metanotum somewhat produced medially. Tegula with distinct moderate-size tubercle; wings with outer surface somewhat irregular but without tubercles. Each coxa with small apicoventral tubercle; each trochanter with larger apicoventral tubercle; fore and hind femora with basal, pointed swelling; fore- and midtibiae each with small rounded basal swelling on outer surface; hind tibia with elongate, pronounced basal tubercle on outer surface; foretibia with distinct apical tubercle on outer surface; midtibia with smaller tubercle in same position; hind tibia without distinct apical tubercle.

METASOMA: Integument with fine regular spicules in many areas; setae absent. Tergum I with a few small rounded tubercles forming transverse band near posterior margin; terga II–IV with transverse bands of small rounded tubercles near posterior margins; tergum V with fewer such tubercles; tergum VI without tubercles; sterna without tubercles; apex of metasoma rounded, not produced as elongate apical spine.

MATERIAL STUDIED: 2 female pupae, 18 mi west of Blythe, Riverside Co., California, collected May 1, 1992, preserved as pink-eyed pupae May 7, 1992 (J. G. Rozen).

DISCUSSION

To what extent do rophitine bees share biological and/or larval synapomorphies with the Halictinae and Nomiinae? This question has been addressed with limited success by Torchio et al. (1967) and Eickwort et al. (1986). This is due in part to the fact that little information was available for the Rophitinae, many of the features of the Rophitinae appear to be plesiomorphic, and comparative data especially concerning the Nomiinae have yet to be compiled.

There is a considerable body of organized data on the nest architecture of the Halictinae (Sakagami and Michener, 1962; Eickwort, 1969; Eickwort and Sakagami, 1979; and references therein). The nest patterns of the Nomiinae have not been so thoroughly studied although a number of papers (Hirashima, 1961; Stephen et al., 1969) give useful information concerning a number of taxa. The nest patterns of these two subfamilies are highly variable and, at least in the Halictinae, of potential value in phylogenetic analysis (Eickwort and Sakagami, 1979). However, the nests of the Rophitinae fall into one basic primitive type that is also found in the other two subfamilies as well as in a number of other families of bees. At this time, gross nest architecture seems of no value for phylogenetic interpretation of the Rophitinae.

Other aspects of nesting biology of the ro-

phitines appear to be specialized. If homologies can be found among taxa outside the subfamily, conclusions about relationships may be forthcoming. The three most noteworthy specializations of the Rophitinae are:

1) Nonreflective, more or less water absorbent cell walls. Cell walls of the other two subfamilies are shiny and water repelling, a feature that seems to be plesiomorphic since lining of cells in many families of bees are shiny.[6] The nonreflective nature of the lining should not be interpreted to mean that rophitine cells are unlined. If cells were truly unlined, then the polarity of this character might well be questioned. However, the fact that water droplets on the cell wall are absorbed more slowly than those placed on the surface of the substrate suggests that a nonshiny lining of some sort is normally applied (but perhaps not in *Conanthalictus*). A lining was detected in the case of *Sphecodosoma*, reported here. Furthermore, the very smooth nature of the rophitine cell surfaces seems to suggest the same; bee cells that lack a lining (e.g., *Hesperapis trochanterata* Snelling, Rozen, 1987; *Parafidelia pallidula* Cockerell, Rozen, 1977) tend to have rough walls.

2) Early pollen-nectar loads shaped into small spheres to which are added subsequent loads. With most bees, early loads of provisions are normally dumped as irregular masses into open cells; shaping of the food loaf takes place only after the final load is brought into the cell.

3) Young larvae ambulatory as they feed around food mass and consequently food mass remaining spherical (except toward end of consumption) as it decreases in size. This feature is associated with pronounced, posteriorly directed ventrolateral tubercles on most of the body segments of the early instars as well as with an abdominal segment X used as a dorsally directed pygopod. This behavior and the associated anatomical features are apparently unknown in either the Halictinae or Nomiinae and are uncommon or absent in other families of bees. Young larvae in these two subfamilies consume the food masses along one side so that the loaves quickly become asymmetrical as seen in side view.

When Eickwort et al. (1986) described the larva of *Dufourea*, they found no synapomorphies of the mature larvae that linked rophitines with the other two halictid subfamilies. The present study demonstrates that one of the rophitines, *Conanthalictus*, does not spin a cocoon with salivary silk. Like the mature larvae of the Nomiinae and Halictinae (none of which spin cocoons), its larva also has a recessed labiomaxillary region, reduced palpi, missing salivary lips, and an undivided labiomaxillary region. Although such similarities cannot be totally dismissed as synapomorphies, such reductions have occurred one or more times in the Colletidae and Melittidae and numerous times in the Anthophoridae, all in conjunction with loss of cocoon spinning. It seems likely that loss of cocoon spinning with the anatomical reductions has taken place de novo within the rophitine clade that is defined by the larval synapomorphies of 1) paired conical dorsolateral tubercles on most body segments and 2) tubercles of prothorax reduced (compare with those of rest of thorax) or absent. For the time being then, one of the conclusions of this paper, like a conclusion in Eickwort et al. (1986), is that the placement of the Rophitinae in the Halictidae continues to rest on adult morphology (e.g., Michener and Greenberg, 1985) rather than on larval anatomy and nesting biology.

Eickwort et al. (1986) compared in detail the biologies and larvae of the Rophitinae with those of the Melittidae and the andrenid subfamilies Andreninae and Panurginae to seek evidence of phylogenetic relationships. The present study does not add sufficient evidence to make a phylogenetic analysis of these similarities worthwhile at this time, but certain additional features have now come to light. These, listed and evaluated as follows, should be added to the characters mentioned by Eickwort et al. (1986) in preparation for such an analysis.

1) Early pollen-nectar supplies shaped into small spheres. This appears to be the case for the rophitines where data have been collected (although for *Dufourea novaeangliae*, only

[6] In his review of this manuscript, Geroge C. Eickwort (in litt.) pointed out that the conspicuous shiny cell linings of Halictinae + Nomiinae may not be plesiomorphic because lactone contents suggest a separate origin in the two subfamilies.

intermediate loads were so shaped, Eickwort et al., 1986). Shaping of early loads is a feature that has been reported both for certain Panurginae (Rozen, 1989) and for *Hesperapis* (Melittidae) (Rozen and McGinley, 1991), always in association with spherical food masses. Because this behavioral feature at least in the Panurginae is restricted to tribes thought to be specialized on the basis of adult and other behavioral features, this similarity between the panurgines and rophitines is thought to be the result of evolutionary convergence and not an indication of relationship.

2) Noncocoon-spinning larvae. The larva of *Conanthalictus conanthi*, as reported here, does not spin a cocoon, a feature shared with all of the Andrenidae as well as with many of the Melittidae. As stated above, this is not considered to be the result of sister-group relationships of these taxa at this time, and associated larval similarities (loss of salivary lips, reduced palpi, recessed labiomaxillary region) likewise are convergences.

3) Paired tubercles arising from labral disc of mature larvae. This feature is a synapomorphy of the Panurginae (McGinley, 1987) and is also found in *Rophites trispinosus*, presumably the result of convergence.

4) Abdominal segment X of larvae positioned dorsally on segment X, anus more or less dorsal on X, and abdominal segment IX produced ventrally. This complex suite of characters is found in the Rophitinae and also in *Hesperapis* and *Capicola* of the Melittidae (Rozen and McGinley, 1974). Its function may be for locomotion, that is, a pygopod, but, as mentioned above, it may also be involved with applying a hardening (and waterproofing?) substance to the cell wall. Because of its structural complexity, it would seem to be a strong synapomorphy (although anatomical details of this modification have not been fully explored to determine homologies). However, there is a suggestion that the similarities may actually be convergences resulting from the fact that the larvae overwinter in cells that have not been completely waterproofed by the female bee. Noteworthy here is the fact that mature larvae of *Neopasites* (Rozen, 1966), *Biastes* (present study), and *Townsendiella* (Rozen and McGinley, 1991), nomadine cleptoparasites associated with these two groups, also have produced venters of abdominal segment IX. Similarly, mature larvae of *Neolarra* (Rozen 1966) from *Perdita* cells (also unlined) have this modification of the abdominal segment IX. Other larval Nomadinae do not have a ventrally protruding abdominal segment IX. There is a possibility that this feature in the cleptoparasites is a synapomorphy of a restricted group rather than a character state that has arisen a number of times. Nonetheless, the correlation of larval host anatomy, larval parasite anatomy, and brood cell features is suggestive that larvae of very different groups have independently evolved similarities in response to the same environmental factors.

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